

# *LABIDOCERA* (COPEPODA, CALANOIDA): NEW AND POORLY KNOWN CARIBBEAN SPECIES WITH A KEY TO SPECIES IN THE WESTERN ATLANTIC

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## A B S T R A C T

Two new species of marine planktonic copepods, genus *Labidocera*, and the hitherto unknown male of *L. panamae* are described. The new species were collected separately from nearshore waters off the West Indian islands of Barbuda and Antigua. Males of *L. panamae* accompanied by females and various juvenile copepodid stages were found near Cape San Blas, Panama. The three species are assigned to the *Labidocera jollae* species group.

The unusual spermatophore morphology found in one of the new species is characterized. The coupler of this spermatophore type fails to cover the female genital pore, and spermatozoan passage to the genital pore is considered relative to gelatinous secretions common to pontellid spermatophores. A key to the species of *Labidocera* found in the western North and South Atlantic oceans and the Caribbean Sea is presented.

The *Labidocera jollae* species group, a product of an exclusively American radiation, consists of coastal water species of planktonic copepods occurring off the eastern and western coasts of the Americas in tropical to warm temperate zones. This group appears to be unusually speciose in the WTNA, i.e., the western tropical North Atlantic region encompassing the Caribbean Sea, the Gulf of Mexico and contiguous sectors of the western North Atlantic Ocean. Four short-ranged species are known from previous studies, based on small sporadic collections scattered unevenly across the region (Fleminger and Moore, 1977). I now report the discovery of two more WTNA species belonging to this extraordinary lineage.

The new species were found in a handful of plankton samples collected at the West Indian islands of Barbuda and Antigua. As with the previously described species from the WNTA the new forms are highly distinctive and yet unmistakably close in genealogy. The specificity of each is indicated by positive qualities, as well as by the absence of evidence of intergradation. Diagnostic features of the six species do not vary appreciably within or between samples. Notably five of the species have been collected at similar localities from 5 to 50 years apart. For example, the new records of *L. panamae*, reported below are separated from the type locality by about 70 miles and were obtained 15 years later. Increasing the number of coastal localities sampled has failed to alter the picture of a separate, independent range for each form. These species have been taken by plankton nets fished at or near the surface in company with a spectrum of typically coastal to broadly neritic planktonic copepods widely distributed in the WTNA. The origins of this unusual regional concentration of apparent sister species living planktonically will be discussed elsewhere.

The western Atlantic is known to contain six additional species of *Labidocera* which have phylogenetic affinities other than with the *jollae* group (Fleminger, 1975; Fleminger and Moore, 1977). A regional key to the described species of *Labidocera* found off the eastern coasts of the Americas follows description of the new forms.

The spermatophore in *L. barbudae* n. sp. described below, is of the unusual type found in *L. barbadiensis* Fleminger and Moore (1977). Though cemented to

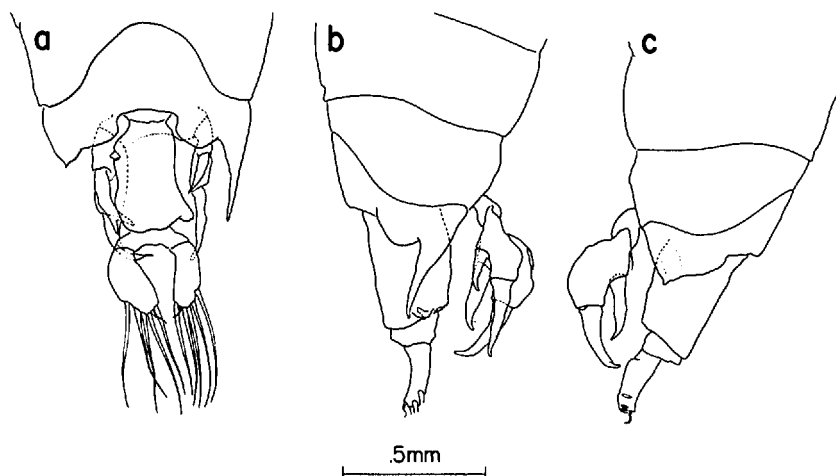


Figure 1. *L. barbuda* new species, adult female, urosome and posterior segments of thorax; a, dorsal view; b, right lateral view; c, left lateral view; furcal setae complete in a.

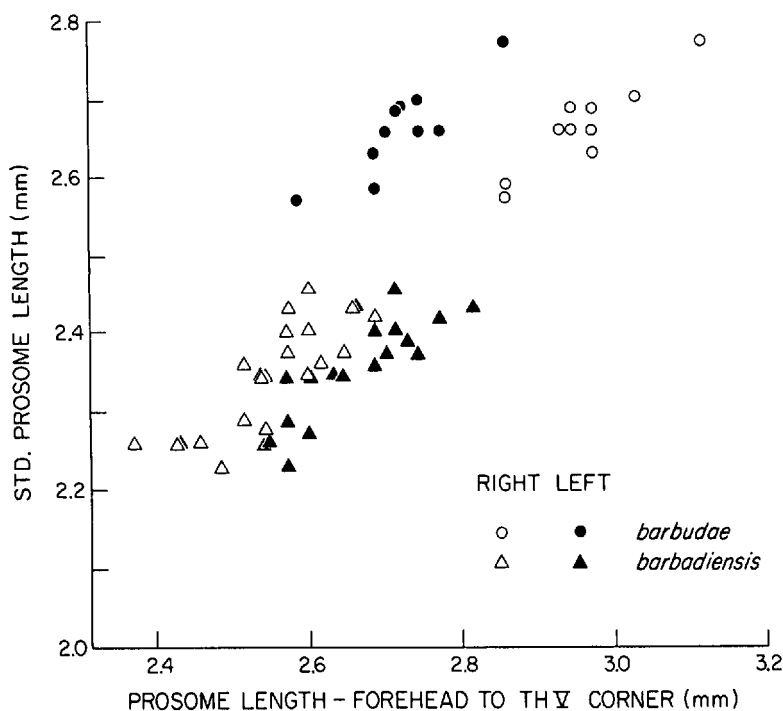


Figure 2. Comparison of length of left and right posterior spiniform processes of fifth thoracic segment (ThV corners). Lengths of processes measured in dorsal view at 50 $\times$  magnification as part of non-standard prosome length from anterior limit of forehead to apex of ThV corner and plotted against standard prosome length measured similarly along mid-sagittal plane to posterior limit of ThV. Symbols: circles—*barbuda*, triangles—*barbadiensis*, open symbols—right side, filled symbols—left side.

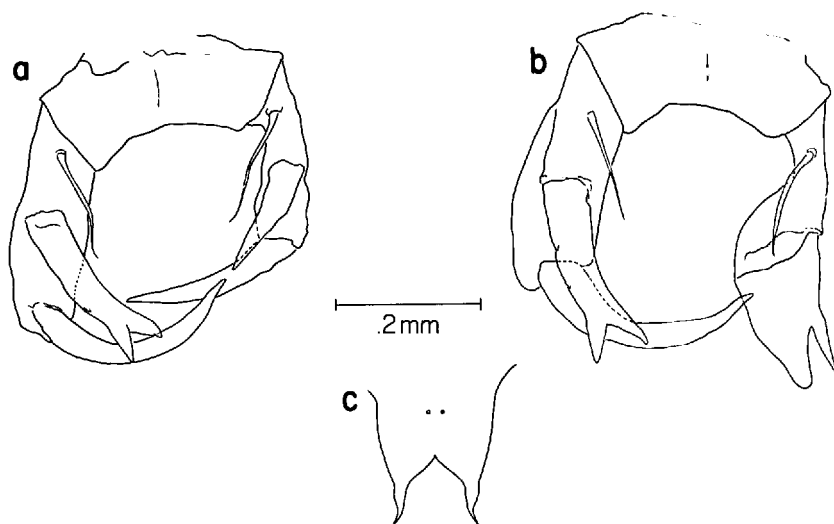


Figure 3. *L. barbudae* adult female; a, fifth legs, posterior view; b, fifth legs abnormal, posterior view; c, rostrum, frontal view.

the genital segment, the coupler apparently fails to cover the genital pore, raising questions as to how sperm attain contact with eggs in the usual course of fertilization. Lee (1972) and Blades (1977) believe a similar spermatophore-genital pore relationship prevails in *Centropages typicus*. Conflicts with their views arising in the course of comparisons between *C. typicus* and the new species are discussed under the heading "Remarks on spermatophore morphology" in the description of *L. barbudae* n. sp.

Abbreviations used in the text to refer to anatomical structures are from the list offered by Rose (1933: p. 19).

### *Labidocera barbudae* new species

#### Figures 1-11

**Material.**—166 ♀♀, 46 ♀♀ with spermatophore, 144 ♂♂, 43 st. V, 1 st. IV juveniles, collected at Sta. 84-56, Smithsonian-Bredin Exped., 5 Apr. 1956, roughly lat. 17°37'N, long. 61°53'W, off Oyster Pond Landing, Barbuda, nightlight sampling 1900 to 2030 h. U.S.N.M. Acc. No. 208263.

**Types.**—Types have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Female holotype, U.S.N.M. Cat. No. 169188; male allotype, U.S.N.M. Cat. No. 169189.

**Measurements.**—Following procedures of Fleminger (1967):

Total Length, mm				Prosome-Urosome Length Ratio		
Adult	$\bar{x}$	range	s	no.	med.	range
♀	3.221	3.12-3.32	.0518	25	4.7	4.3-5.0:1
♂	3.097	2.88-3.21	.0755	25	5.4	4.5-5.6:1

**Description.**—Most similar morphologically to *Labidocera barbadiensis* Fleminger and Moore; diagnostic features concentrated in sexually modified structures.

**ADULT FEMALE:** Thoracic segments IV and V (ThIV, ThV) separated by continuous articulation suture. Right posterior corner of ThV extending posteriad as an attenuated spiniform process reaching as far as posterior end of genital segment;

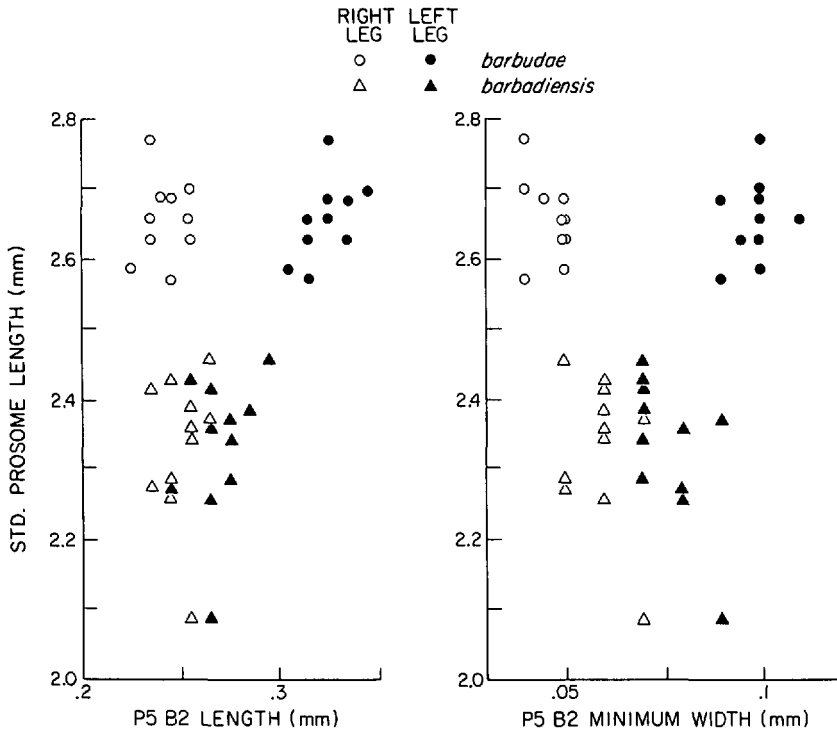


Figure 4. Comparison of maximum length and minimum width of basis (B2) of right and left fifth legs (P5) in adult females of *L. barbuda* and *L. barbadiensis*. Maximum length of B2 taken in posterior view from proximolateral corner to distalmost limit. Minimum width of B2 taken in posterior view normal to length of segment at distal limit of insertion of seta. B2 measurements taken at 100 $\times$  magnification, standard prosome length taken at 50 $\times$  magnification. Symbols: circles—*barbuda*, triangles—*barbadiensis*, open symbols—right B2, filled symbols—left B2.

left posterior corner much shorter, extending to position of genital pore and ending in a small denticle (Fig. 1a-c); in *barbadiensis* left ThV corner longer than right side (Fig. 2) and produced in a robust cone. Genital segment in dorsal view with prominent tubercle extending laterad from right posterior corner opposing apex of right ThV corner (Fig. 1a); genital pore proximal and on left side, i.e., opening lateral as in *barbadiensis*.

Anal segment short and caudal furca moderately asymmetrical as in *barbadiensis*.

Fifth Legs (Fig. 3a): P5 with quality characterizing the Caribbean lineage of the Labidocera jollae group, namely exopod shorter than endopod; B2 with distance between articulations of endopod and exopod almost equal to distance between proximal margin of B2 and articulation with exopod. New species with more pronounced asymmetry in B2 and in the rami, left side being about  $\frac{1}{3}$  longer and in posterior view much wider at proximal end, right side with a medial notch or constriction near base of seta thereby narrowing segment to about half that of left B2 measured similarly (Fig. 4), asymmetry evident in lateral view as well (Fig. 1b,c); right B2 smaller than left but difference much less in *barbadiensis* (Fig. 4). Left exopod terminating in pair of strongly divergent spines of equal length, apex of right exopod pointed but not bifurcated; apices of exopods more like the condition in *wilsoni* and *panamae* than in *barbadiensis*, the lattermost

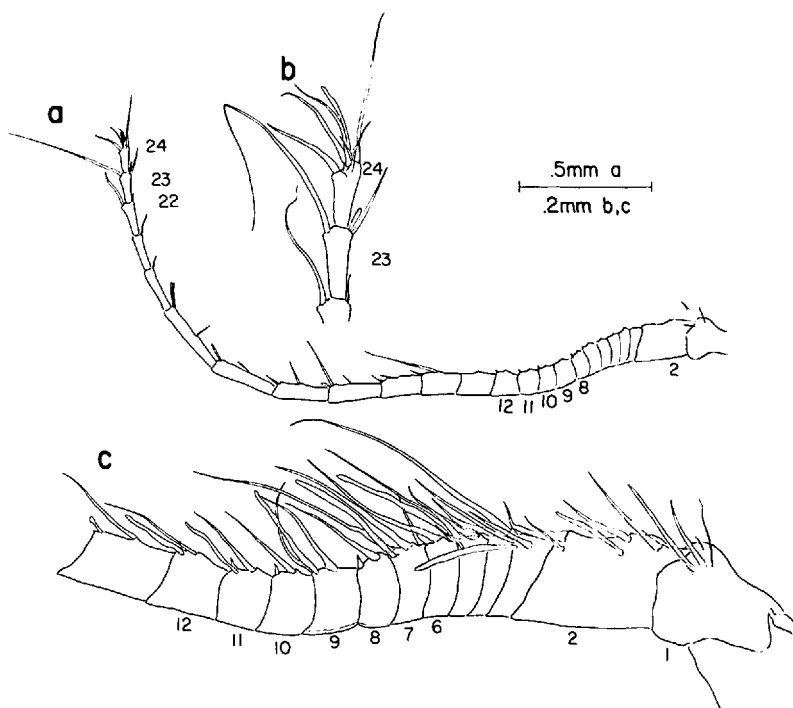


Figure 5. *L. barbudae* adult female, right first antenna, ventral view; *a*, habitus, many setae omitted; *b*, terminal segments; *c*, proximal segments showing cuticular thickening and shallow notch characterizing posterior edge of segments 8 and 9 as well as short dentiform setae of segments 8, 10, 11 and 12.

with both exopods apically bifurcated into unequal spines. Left endopod more strongly curved than right as in *barbadiensis*. One specimen was seen with an aberrant uniramous right leg (Fig. 3b), specimen otherwise similar to others on hand; teratological right P5 is probably a product of an ontogenetic accident.

Rostrum as in *barbadiensis*, in lateral view base wide and processes not longer than base, in frontal view processes separated by a triangular notch (Fig. 3c).

First Antenna (Fig. 5a-c): A1 as in other Caribbean species of the jollae group, showing specialization affecting the articulation of segments 8 and 9 which are fused in the Pacific species (Fleminger, 1967). The specializations in the Caribbean lineage exemplified by *barbudae* are seen in dorsal and ventral views: a weak constriction and partial fusion of the posterior margin at the junction of segments 8 and 9 (Fig. 5c). Unique short dentiform setae are found antero-distad on segments 8, 10, 11 and 12 as in all other species of *Labidocera* I have examined (Fig. 5c); segments 6 and 7 are totally separated by an articulation suture as in all other members of the jollae group; these segments are partially to fully fused in most other species of *Labidocera* seen by me.

Meristic details of the swimming legs agree with those reported for *wilsoni* by Fleminger and Tan (1966).

Spermatophore, i.e., coupler and sperm chamber, generally resembles that in *barbadiensis*. Lateral plates of coupler in new species shows several diagnostic differences; left plate unattached to urosome extending posteriad and below left furcal ramus before turning and curving upward to terminate as a vertical plate between the two furcal rami (Figs. 6a,b, 7b). Right plate of coupler wrapped

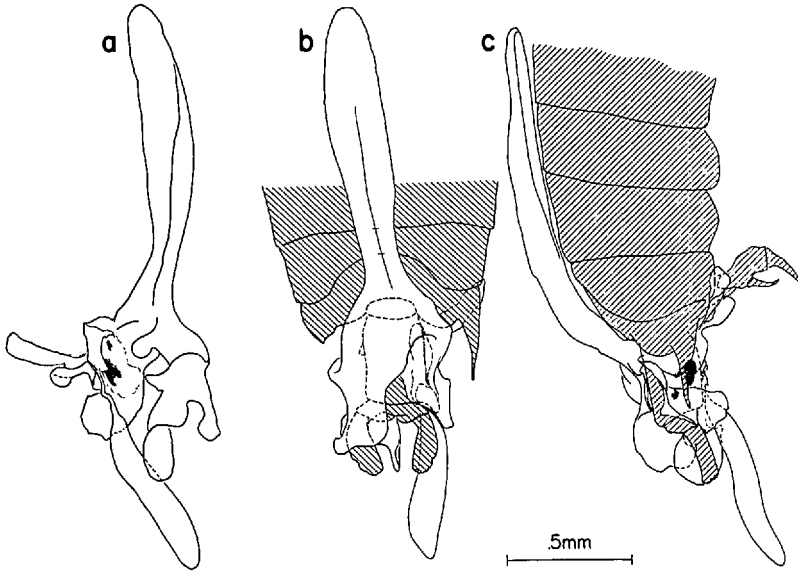


Figure 6. *L. barbudae* spermatophore. Stippled area indicates sperm in blister-like chamber formed by inner and outer walls of coupler, exoskeleton shaded by diagonal lines; a, left ventrolateral view after removal from female; b, dorsal view; c, right lateral view.

around right and ventral sides of genital segment as a broad shield extending toward but not quite reaching genital pore, posterior portion extending laterally from urosome and loosely covering proximal portion of tubular sperm chamber (Figs. 6a–c, 7a,b). Anchor-like process extending from right side of coupler and embracing genital segment ventrally in *barbadiensis*; extending antero-ventrad to right in new species and terminating beneath thorax (Figs. 6c, 8a). Sperm chamber extending posteriad usually beneath furca and varies from left to right side. Genital pore not covered by firm cuticular material of the coupler in all specimens examined (no. = 45) though ventral margin extending from right side terminating variously close to genital pore (Fig. 7a,b). In *barbadiensis* ascending arm of anchor-like clasper ventral to urosome and originating on right side partially over-

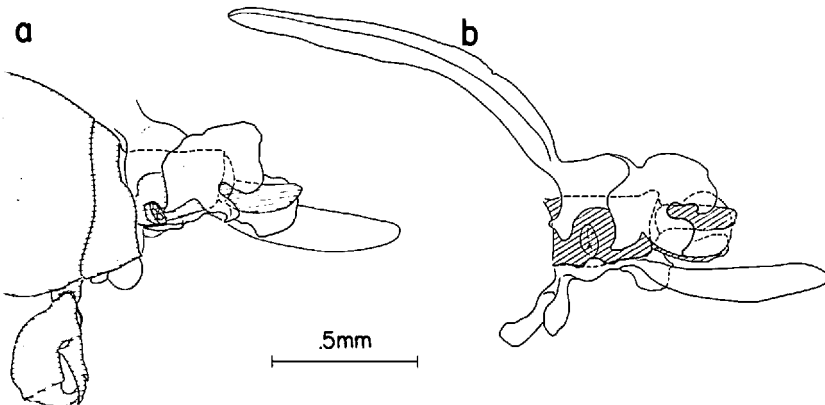


Figure 7. *L. barbudae* spermatophore coupler showing relationship to genital pore, exoskeleton shaded by diagonal lines; a, left lateral view; b, left ventrolateral view, another specimen.

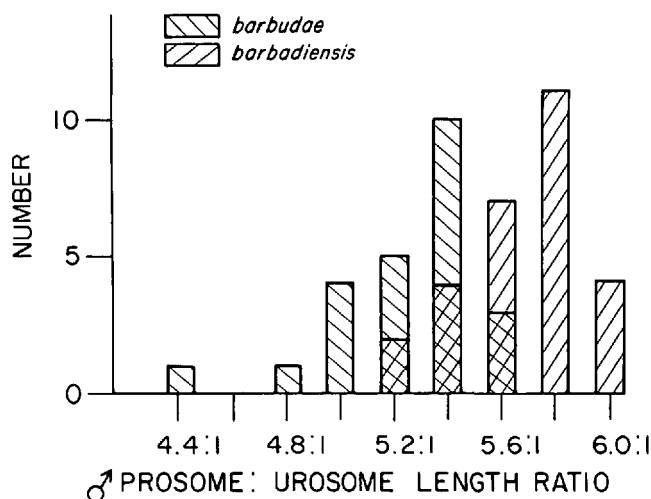


Figure 8. Frequency distribution of prosome-urosome length ratio in adult males: *barbudae*—diagonal lines rising to left; *barbadiensis*—diagonal lines rising to right.

laps genital pore; vertical plate found between the furcal rami originates from right side of coupler and enters furcal area from above while the unattached plate extending ventrad to left of urosome terminates at that place.

**ADULT MALE:** Most similar to *barbadiensis*. PUR smaller, TL larger than in *barbadiensis* (Figs. 8, 9); larger proportional length of prosome in new species appears to be result of a relative decrease in length of furcal rami. Length proportions of P5 to body (Fig. 10a) and appearance of A1, P2, P4 similar to those in *barbadiensis*.

**Second Pair of Swimming Legs:** Right exopod with Re2 bearing elongated tubiform Se bent about 90° laterally (Fig. 10b) as in *barbadiensis*.

**Fifth pair of legs** with distinctive features concentrated in chela and the left ramus. Fixed finger (proximal segment or Re1) of chela (Fig. 11a,b) lacking proximal pair of robust processes found in *barbadiensis* opposing apex of movable finger (distal segment or Re2 and Re3 fused); in new species proximal processes replaced by a low bilobed tubercle (Fig. 11b); fixed finger with two larger processes distal to sensoriiform seta, the proximal one elongated, ridge-like and about half the length of the fixed finger, the distal one a falciform lamella similar to that in *wilsoni*; movable finger attenuated, when adducted reaching to articulation between proximal finger and B2. Chela with total of five visible sensoriiform setae as in other species of the group, omitting one usually fused to apex of movable finger but separate in some species (unpublished).

**Apical segment of left P5** (Fig. 11a) similar to that in *barbadiensis* except for distance between articulations of Se1 and Se2, in new species this distance about twice the length of the apical digitiform process; in *barbadiensis* this distance roughly equals length of apical process. Proximal segment of left exopod curving medially about 50° (Fig. 11a); in *barbadiensis* curvature largely confined to sharp bend at mid-length of segment.

**Etymology.**—The specific name *barbudae* refers to Barbuda Bank located at the northern end of the West Indies and the geographical site of the species' type locality.

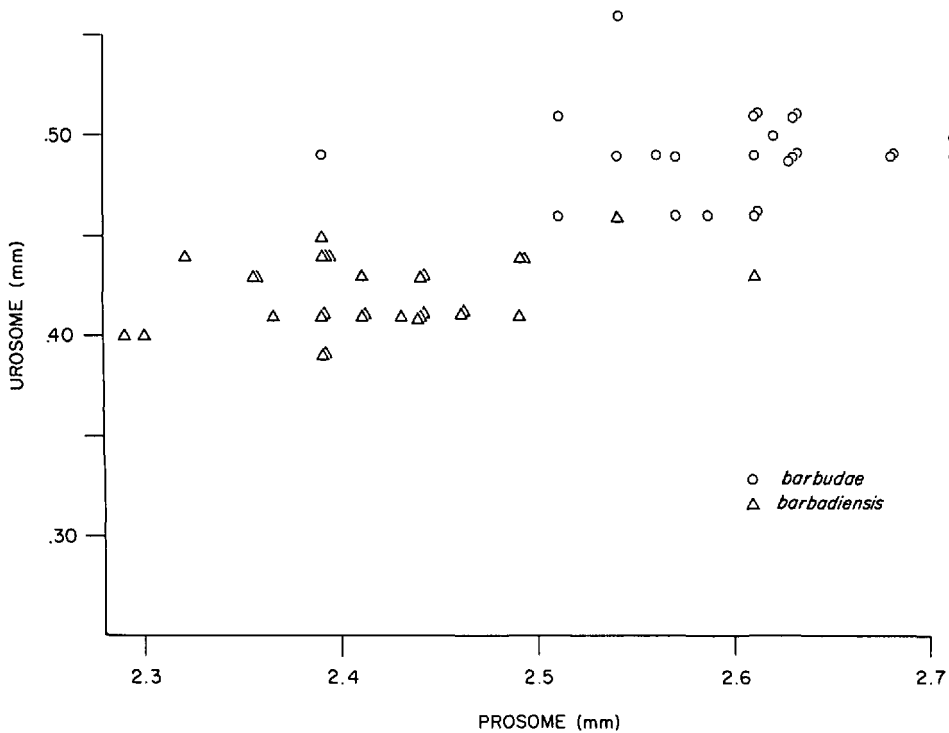


Figure 9. Standard prosome length plotted against standard urosome length of adult males: circles—*barbudae*, triangles—*barbadiensis*.

*Remarks on Spermatophore Morphology.*—Agitating and removing the spermatophore from the urosome of about 30 specimens of *barbudae* n. sp. and *barbadiensis* revealed that the attachment of the coupler to the genital segment is neither widespread nor sporadic. In fact only a small area of the coupler is actually cemented to the genital segment. The place of attachment on the genital segment is not only restricted to a small area, but also differs in the two species. In the new species the right plate of the coupler is cemented to the right side of the genital segment, while in *barbadiensis* the dorsal plate is cemented to the dorsal side of the genital segment. These differences follow the pattern seen in other American labidocerans whereby coupler morphology and place of attachment tend to be more distinctive, and often species-specific, among species of the same species group with adjacent or overlapping ranges than between allopatric species (Fleminger, 1975). Lee's (1972) account of spermatophores in Atlantic-Mediterranean neritic species of *Centropages* indicates the presence in that genus of a similar pattern.

In both *barbudae* n. sp. and *barbadiensis* the sector of the coupler attached to the genital segment has an inner and outer layer. The inner layer is rigidly cemented to the genital segment. The outer layer forms a blister-like chamber separated from the inner layer and apparently rejoins the inner layer beyond the limits of the cemented sector. The blister-like space between the layers also forms a distinctive passageway between the short neck of the sperm chamber and the edge of the coupler adjacent to the genital pore. Concentrations of sperm found within the passageway in a number of specimens attests to the open communi-



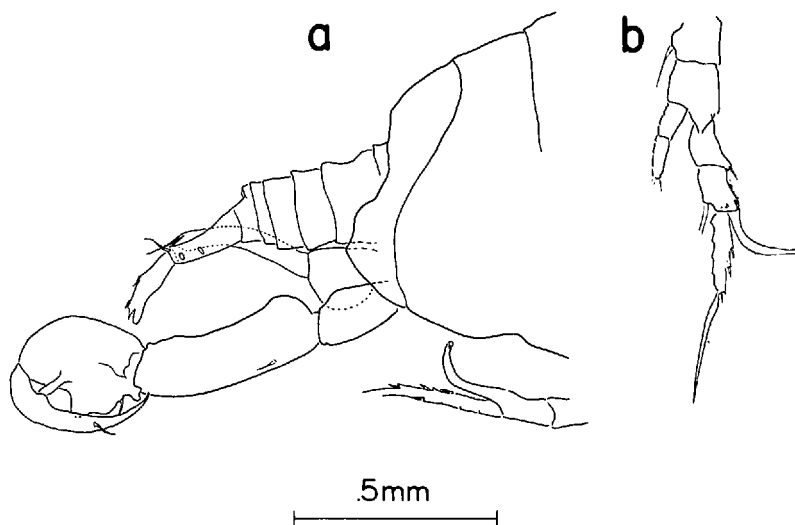


Figure 10. *L. barbudae* adult male; a, right lateral view of urosome, posterior segments of thorax, second and fifth legs; b, right leg of second pair, posterior view; most setae omitted.

cation between it and the sperm chamber. The blister-like sperm chamber resembles in principle the ventral sac, a secondary sperm chamber found in *Centropages furcatus* by Lee (1972) which he also termed an external "spermathecal sac."

Notably in both *barbudae* n. sp. and *barbadiensis* the coupler in preserved specimens does not cover the genital pore and thereby provide a shield for sperm in transit from the sperm chamber to the internal seminal receptacles (spermathecae). A shielded passageway is apparent in the three Pacific species of the jollae group where the coupler totally envelops the genital pore (Fleminger, 1967, Figs. 1g, 3h, 6g,h).

Lacking any indication of artifacts in spermatophore morphology introduced by preservation, I am inclined to accept the gap between the genital pore and the termination of the firm cuticular portion of the coupler as natural and characteristic of these West Indian species. In *wilsoni* I have observed a conduit (fertilization tube ? or stalk) extending from the sperm chamber and reaching beyond the coupler to the genital pore to which it was cemented (Fleminger and Tan 1966, Fig. 1g). This condition was not seen in *barbudae* n. sp. or *barbadiensis*.

Regions of the female urosome covered by the spermatophore coupler were examined with the aid of a light microscope at magnifications of 100 to 600 times. Cleared intact specimens and others with tissues removed by KOH (Fleminger, 1973) were scanned. No openings or conduits internal or external were found apart from the genital pore that might serve to bring the sperm into contact with a mature egg prior to its passage through the genital pore. Cuticular pores were seen (about 1.5 to 3  $\mu\text{m}$  across) that are the discharge sites of tegumental glands. They were, in fact, most numerous at the place where the coupler was cemented to the urosome (in preparation).

In view of the rapid irreversible chemical changes in spermatophore contents exposed to seawater (Park, 1966) and the lack of motility in crustacean spermatozoa it is likely that the pontellid spermatophores usually seen in preserved specimens may not represent the entire functioning organ. That is, in addition to

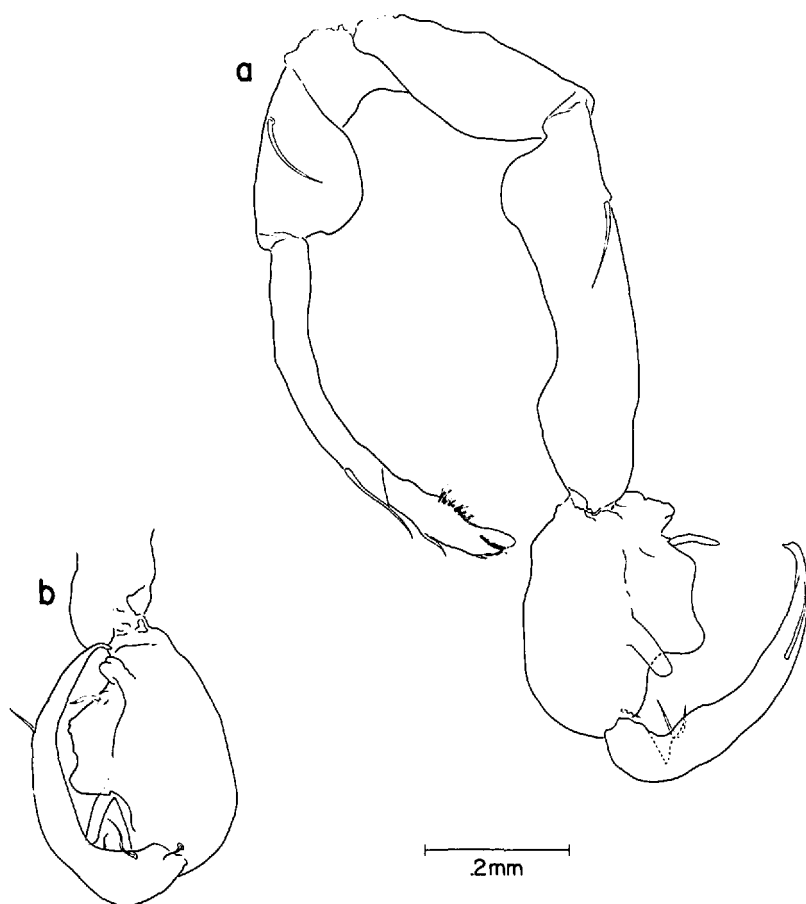


Figure 11. *L. barbudae* adult male fifth legs; a, posterior view; b, chela, anterior view.

the firm cuticular portion of the spermatophore, there may be a portion that does not preserve well in routinely handled plankton samples. Indeed, this may be the function of the protective jelly coat found by Park (1966) in *Epilabidocera amphitrites* (= *longipedata*). On a number of occasions I have observed a similar jelly coat surrounding the spermatophore and urosome in *L. trispinosa*, *L. johnsoni* and *L. lubbocki* in living and carefully preserved material. As Park notes for *Epilabidocera*, the jelly coat is highly transparent and quite delicate. It deteriorates or erodes within hours after mating. In preserved samples it is sticky, rather shapeless and usually obscured by debris adhering to its surface. The jelly coat is also highly susceptible to mechanical damage. In the species mentioned above, the jelly coat expands immediately after attachment of the spermatophore and surrounds the urosome as an ellipse-like body. Among several possible functions, it could provide a protected passage for sperm to travel from cuticular coupler to genital pore in species in which the coupler typically fails to cover the genital pore.

It has been reported (Lee, 1972) that the spermatophore coupler fails to cover the genital pore in *Centropages typicus* Krøyer. Working with preserved specimens, Lee expressed the view that spermatozoa enter the second urosomal segment through a "seminal pore" whose presence he postulated as being at the site

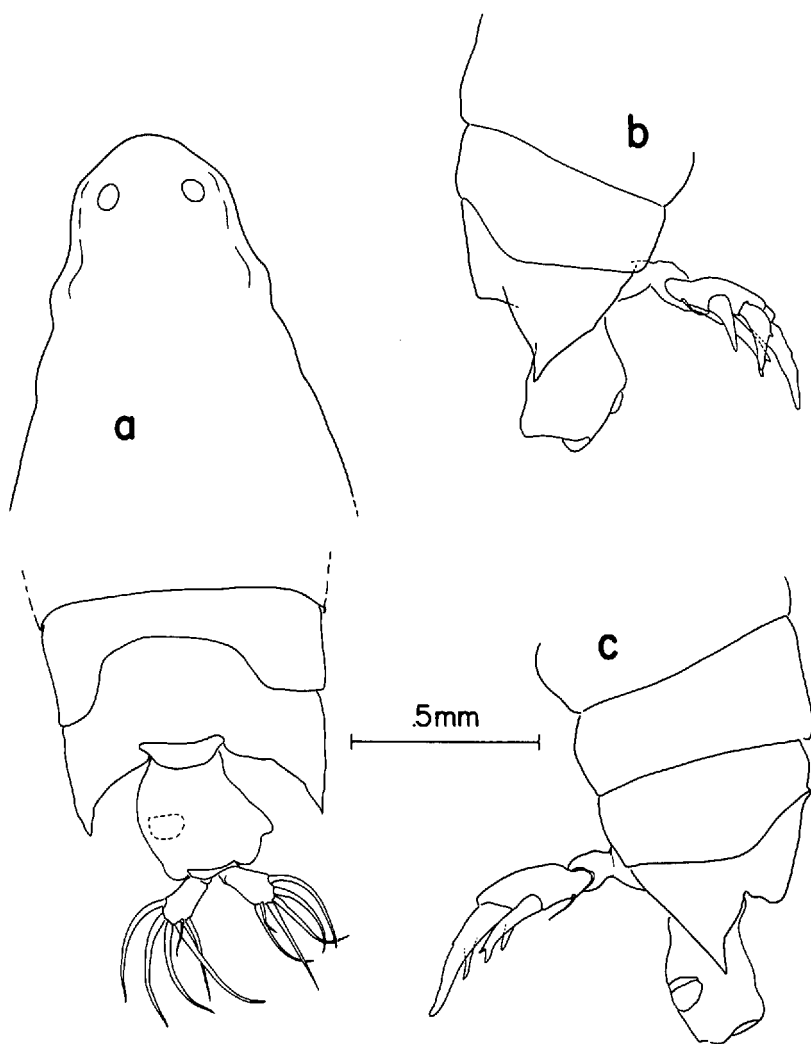


Figure 12. *L. antiquae* adult female; a, dorsal view, middle segments of thorax omitted; b, right lateral view of posterior thoracic segments, genital segment and fifth legs; c, left lateral view of b.

of attachment of the spermatophore stalk, an elongation of the neck of the sperm chamber. He did not demonstrate the opening, passage of the spermatozoa through the cuticle wall, or the manner by which spermatozoa transit internally to the gonopore-oviduct juncture where existing eggs may be fertilized. Blades' (1977) direct observations of mating pairs of *C. typicus* reveal that the spermatophore may in fact provide a continuously protected conduit for spermatozoa to reach the genital pore directly without entering the second abdominal segment. Contrary to Lee's implicit assumption that the anterior coupler in this species is relatively functionless, in view of its shapeless appearance in preserved specimens, Blades observed in freshly mated females that the "... anterior coupler fits loosely around the lateral and ventral surfaces of the first segment."

I have examined the urosome of preserved spermatophore-bearing specimens of *Centropages typicus* collected at several localities in the northwest Atlantic.

As in the case of *barbudae* n. sp. and *barbadiensis* mentioned above, microscopic examination was carried out in search for pores and conduits that would provide sperm with access to the genital field. No structures were seen that could be identified as the opening of the alleged seminal pore or subcuticular conduits for sperm to travel to the genital field. The pores that were observed were determined on the basis of their size and proximity to integumental glands to be the openings in the exoskeleton that Lee (1972, pl. II) referred to as cement glands. The anterior coupler in *C. typicus* should be examined more closely to ascertain if it aids in conducting spermatozoa to the genital pore, the only apparent external place of entry into the female reproductive tract found in *Centropages* and *Labidocera*.

*Phylogenetic Relationships and Sympatry.*—The new species and *barbadiensis* present an interesting morphological contrast in similarity and difference. They diverge in a handful of characters that probably function during mating. In the female, elongation of one ThV corner shifts from the right side in the new species to the left side in *barbadiensis*. The tubercle on the right side of the genital segment in *barbudae* n. sp. opposing the long spiniform right ThV corner has a counterpart in the strong asymmetry of the left furcal ramus opposite the enlarged left ThV corner in *barbadiensis*. The coupler is cemented to the right side of the genital segment in *barbudae* n. sp. but in *barbadiensis* it is attached to the dorsal side. In males, the most pronounced differences are found in the chela of the right fifth leg, the structure holding the female during the process of spermatophore placement.

These differences suggest that the mating position of the male differs in the two species and also that the divergence of these characters may be the outcome of selection against hybridization between the two species. That is, during the speciation process reproductive isolation of the two species was achieved following secondary contact by development or reinforcement of a prezygotic reproductive barrier.

Although the two species have not been found together in the same sample, geographical localities place *barbudae* n. sp. and *barbadiensis* in virtual sympatry. Sampling records of the two species indicate that *barbudae* n. sp. and *barbadiensis* probably have overlapping spatial distributions. *L. barbudae* n. sp. has been found only once several hundred meters west of the lee coast of Barbuda Island. *L. barbadiensis*, initially known from Barbados Island, has been subsequently collected by the author at stations adjacent to the West Indian islands of St. Martin, Antigua and St. Lucia (unpublished data). Antigua and Barbuda are less than 50 km apart and rest on the same submarine basement, namely Barbuda Bank. St. Martin lies about 110 km to the west of Barbuda Bank. *L. barbudae* n. sp. does not appear to range south of Barbuda Island but coastal zooplankton sampling in the Lesser Antilles has been very sparse spatially and temporally. Representative coastal zooplankton samples are also unavailable for testing the possibility that one or both species range westward into the Greater Antilles. Seasonally representative sampling is also required to explore the possibility that these species avoid unfavorable periods by means of a resting stage (e.g., Kasahara, Uye and Onbe, 1975; Grice and Gibson, 1975).

#### *Labidocera antiguae* new species

Figures 12–14

*Material.*—2 adult ♀♀ collected in English Harbor, Antigua, West Indies, Barbados-Antigua Expedition, 1918, State University of Iowa, date, time and sampling method not known, U.S.N.M. Acc.

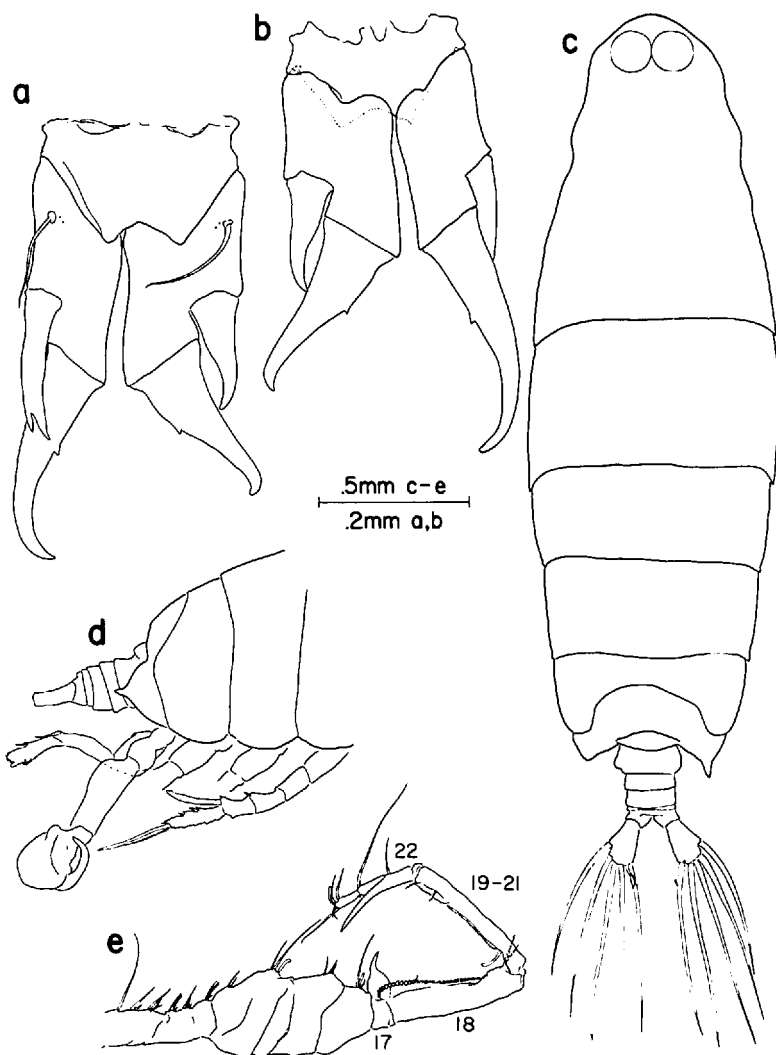


Figure 13. *L. antiquae*. Adult female fifth legs; *a*, posterior view; *b*, anterior view. Basis and rami flattened excessively producing a somewhat unnatural orientation of legs distal to coxa in posterior view. Adult male; *c*, dorsal view; *d*, right lateral view, incomplete; *e*, right first antenna, dorsal view.

No. 131487; 1 ♂, 1 st. VI intersex collected in English Harbor under electric lights off seawall, April 19, 1958, by Smithsonian-Bredin Expedition, stat. 80-58, U.S.N.M. Acc. Nos. 131487, 21737.

*Types*.—Types have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Female holotype, U.S.N.M. Cat. No. 169193; male allotype, U.S.N.M. Cat. No. 169194.

*Measurements*.—Following procedures of Fleminger (1967):

	Total Length, mm	Prosoma-Urosome Length Ratio
♀ 1	3.00	5.5:1
2	2.79	5.5:1
♂	2.69	6.1:1

*Description.*—Showing all characteristics of the jollae group including meristics of swimming legs, morphologically most similar to *wilsoni* and *panamae*.

**ADULT FEMALE:** Posterior corners of ThV similar to those of *wilsoni* but more robust, right side extending posteriad about as far as mid-length of urosome and slightly wider than left side (Fig. 12a–c).

Genital segment asymmetrical; in dorsal view right side with single triangular tubercle about two-thirds from proximal end; right side in *wilsoni* with two smaller rounded tubercles, one near proximal end, the other near distal end of segment; right side in *panamae* with robust bilobed swelling. Left side of genital segment in new species produced in a low rounded swelling (Fig. 12a), similar to the one in *wilsoni*. Genital pore in all three species opening ventrally but weakly displaced to left of center.

Furcal rami symmetrical and otherwise undistinguished as in *wilsoni* except that they are strongly divergent in both available specimens (Fig. 12a); in *wilsoni* rami tend to be parallel.

Fifth Legs (Fig. 13a,b): P5 relatively large in new species; in lateral view (Fig. 12b,c) overall length from origin of B1 to apex of endopod if extended posteriad reaches beyond distal end of genital segment; posteriorly extended P5 in *wilsoni* and *panamae* reach to about mid-length of genital segment; proximal end of B2 in both left and right legs produced in a large rounded shoulder anteromedially beyond articulation with B1 (Fig. 13b).

**ADULT MALE:** In addition to secondary modifications typical of jollae group males, asymmetry of the ThV posterior corners pronounced, right corner being produced as a robust spiniform process extending posteriad to distal end of UI (Fig. 13c,d), left ThV not so modified.

First Antenna: Right A1 (Fig. 13e) as in *wilsoni* except that spur on segment 22 extends beyond distal end of segment 24; in *wilsoni* segment 24 extends beyond distal end of spur.

Second to Fourth Pairs of Swimming Legs: P2 with elongated tubiform Se on Re2 of right exopod almost straight (Fig. 14a), length of Se measured along median border about equal to length of Re3 measured along lateral border; in *wilsoni* this Se with shallow but distinctive bend of about 30° and length shorter than Re3. P3 with Se of Re1 and Re2 asymmetrical, right side being more robust as in *wilsoni*. Right P4 with Se of Re1 and Re2 spiniform and similar to their counterparts on the left leg; in *wilsoni* Se of right P4 Re1 shaped like a cup, Se of Re2 spiniform; in *barbudae* and *barbadiensis* P4 with Se of Re1 and Re2 cup-like.

Fifth legs with diagnostic features on both left and right sides. Chela (Fig. 14b–d) with movable finger relatively short, when adducted not extending beyond proximal process of fixed finger as in *wilsoni* (Fig. 14f); fixed finger with uneven bilobed proximal process, larger process spurlike as in *wilsoni*, smaller process rounded and low in posterior view, lacking in *wilsoni*; with movable finger adducted apex of movable finger rests against shallow notch between two proximal lobes of fixed finger (Fig. 14c); fixed finger with two additional processes similar to those in *wilsoni*. Apical segment of left leg (Fig. 14b,e) with medio-distal digitiform process barely reaching apex of segment; in *wilsoni* this process more distal and extending well beyond apex of segment (Fig. 14f).

*Etymology.*—The specific name *antiguae* is taken from the West Indian island of Antigua and denotes the place of the type locality.

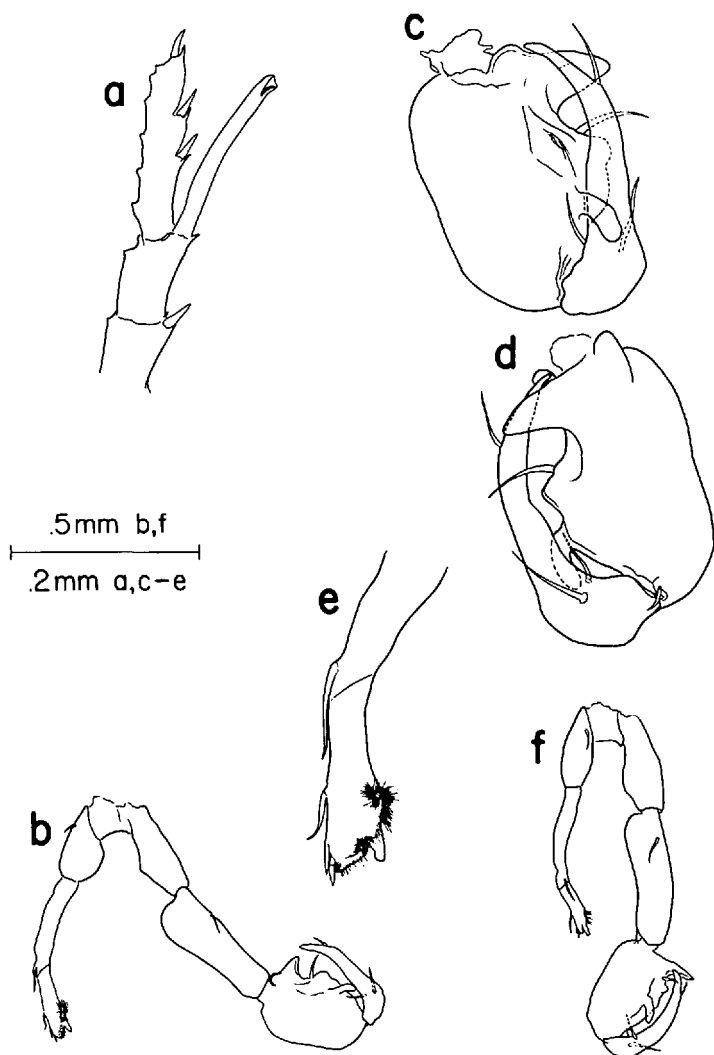


Figure 14. *L. antiquae* adult male; a, exopod of right second leg, anterior view, setae omitted; b, fifth legs, posterior view; c, chela, posterior view; d, chela, anterior view; e, apical segment of left fifth leg, posterior view. *L. wilsoni* adult male fifth legs; f, posterior view.

**Remarks.**—Morphological evidence shows the new species to have close genealogical relationships to *wilsoni* and *panamae*. Character states differ among the three species only in small details (i.e., male: right first antenna, second and fifth pairs of legs; female: fifth pair of legs, genital segment, caudal furca, posterolateral corners of the fifth thoracic segment). Lack of geographical contact correlates with the shallow morphoclines shown by these three species, their known distribution being restricted to widely separated peripheral sectors of the WTNA region. In contrast the characters mentioned above are found to be strongly divergent when comparing the new species and its geographical neighbors, *barbuda* and *barbadiensis*. In fact each of these characters show a steep morphocline in all other sets of parapatric species within the jollae group: i.e., the East Pacific species (Fleminger, 1967) and the northern WTNA species (Fleminger,

1975). This association of geographical proximity and extent of morphological divergence in sexually modified characters is too regular and pronounced to support a premise that selection or drift in allopatry are solely responsible. The correlation is consistent however with the model of parapatric speciation (Key, 1968; Mayr, 1970: 318). In this model secondary contacts between expanding sister populations reinforce pre-zygotic reproductive barriers when interpopulation matings are ultimately less successful for population recruitment than intrapopulation matings. The parapatric speciation model and phylogenetic relationships may provide a framework for inferring major events in the radiation and evolution of the jollae group.

Specimens from two localities in the Gulf of Honduras have been tentatively assigned to the new species. They were collected in shallow coastal waters during daylight hours by zooplankton nets towed between a bottom depth of <40 m and the surface during R/V ALPHA HELIX Amazon-Caribbean Expedition, Phase IX (station 33, 14 July 1977, ~16°05'N, 87°00'W, west of Utila Island, Honduras, total of 28 males, 12 females and various juvenile copepodids; stations 36 and 37, 15–16 July 1977, ~17°12'N, 87°52'W, east of Turneffe Reef, Belize, total of 14 males, 14 females and various juvenile copepodids). Obvious proportional differences in sexually modified structures in both sexes distinguish the Turneffe, Utila and Antigua samples from one another. Differences between the Gulf of Honduras samples are less pronounced than are those between the Honduran and Antiguan samples. For example, the right ThV posterior corner in Honduran females is wider and about twice the length of the left corner, reaching to the right furcal ramus. In Antigua females the right and left sides are almost symmetrical. It is tempting to speculate that this apparent geographical variation is the product of interactions between overlapping southern populations of the new species and *barbudae* in which the female right ThV posterior corner is highly modified and elongated. However, representative samples from the Gulf of Honduras, the offshore banks leading to the Greater Antilles and south to the Lesser Antilles will be required to explore this possibility.

### *Labidocera panamae* Fleminger and Moore

#### Figure 15

*Labidocera panamae* Fleminger and Moore, 1977, Bull. Mar. Sci. 27: 527–8, Figs. 25–30 (type: lat. 09°27'N, long. 79°47'W; U.S.N.M. Cat. No. 156227).

The original description was based on a single female specimen taken at the surface near Cristobal, Panama. Additional material of both sexes and juveniles were found in recent samples from Holandes Cays, Archipiélago de las Mulatas, Panama. The males are assigned to *Panamae* by virtue of their co-occurrence with females and juveniles, their obvious kinship with the jollae species group and the lack of an equally likely alternative assignment.

**Material.**—Total of five males, two females and various juveniles from zooplankton net tows taken between bottom depth of ≈25 m to the surface at station 14, ~9°33.5'N, 78°42.5'W in daylight hours, 30 June 1977, R/V ALPHA HELIX Amazon-Caribbean Expedition, Phase IX.

**Measurements.**—Following methods of Fleminger (1967):

	Total Length, mm		Prosoma-Urosome Length Ratio	
	range	median	range	median
♀	2.63–2.71		4.3–4.7:1	
♂	2.37–2.46	2.43	5.1–5.7:1	5.4:1

**Description.**—ADULT MALE: resembles in part *wilsoni* and *antiguae* and otherwise shows features more like *barbudae* and *barbadiensis*. Thorax in dorsal view



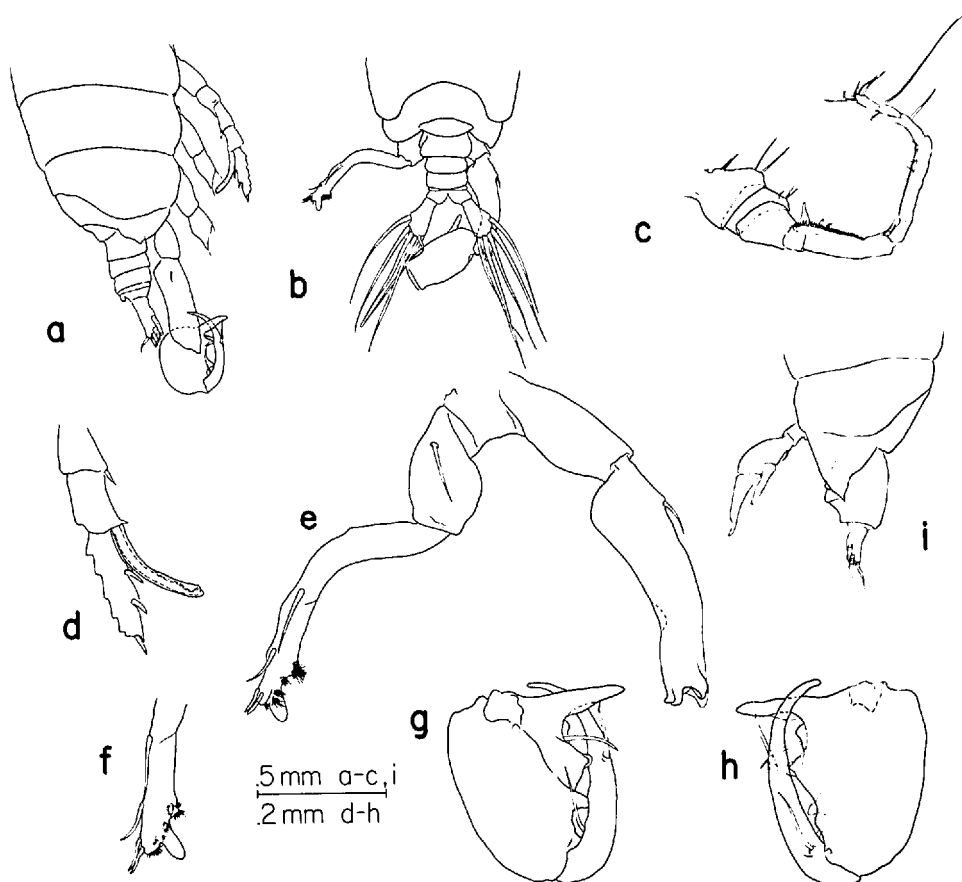


Figure 15. *L. panamae*. Adult male, thorax and urosome; a, right lateral view, segmentation and setation incomplete; b, dorsal view; c, right first antenna, dorsal view; d, right exopod of second leg, posterior view, setae omitted; e, fifth pair of legs omitting chela, posterior view, but terminal segment of left leg imperfect in position; f, terminal segment of left P5, posterior view; g, P5 chela, posterior view; h, same, anterior view. Adult female; i, thorax, urosome and P5, left lateral view, segmentation and setation incomplete.

(Fig. 15b) with ThV posterior corners weakly asymmetrical; right side produced in small knob, in lateral view dorsal border of ThV turns ventrally before knob is produced (Fig. 15a) in *wilsoni* dorsal border straight and ending posteriorly in small knob.

Right First Antenna: as in *wilsoni*; segment 18 and fusion segment 19–21 with uniform row of teeth; spur on segment 22 short, barely extending beyond segment 23 (Fig. 15c).

Swimming Legs: P2 with elongated tubiform spine (Se) on Re2 bent about 50° to lateral (Fig. 15d), this bend in *wilsoni* about 30°; P3 with Se of Re1 and Re2 asymmetrical, those of right side being more robust as in *wilsoni*; P4 with Se of Re1 cup-shaped as in *wilsoni*.

Fifth Legs (Figs. 15e–h): exopod of left P5 with distal half bent medially about 50° as in *barbadiensis*, in *wilsoni* bend less than 35°; terminal segment of left P5 with hirsute medial tubercle and relatively long digitiform process at apex as in

*wilsoni*, but process extending obliquely mediad from apical segment (Fig. 15f), in *wilsoni* this process parallels longitudinal axis of terminal segment (Fig. 14f). Chela of right P5 with movable finger attenuated, when adducted apex reaching articulation of fixed segment and B2 (Fig. 15g) as in *barbadiensis*. Fixed segment with proximalmost process as in *wilsoni* but followed immediately by low lamelliform ridge arising from anterior side of chela (Fig. 15g,h), ridge proximal to large sensoriiform seta suggesting that latter is homologue of anterior proximal process of pair on fixed finger of *barbadiensis*; fixed finger with two processes distal to seta as in *wilsoni* but process near seta broadly triangular and more distal process about as high as wide (Fig. 15g,h); in *wilsoni* first process an irregular tubercular ridge, and second one about twice as high as wide (Fig. 14f).

**Remarks.**—In the original description of the female the dorsal border of the left ThV in lateral view was characterized as being interrupted by an unusual notch anterior to the spiniform apex (Fleminger and Moore, 1977: Fig. 29). In the new material a suggestion of this notch is seen in a bright field of transmitted light but as a feature produced by cuticular folds on the medial side of the corner. In lateral view a shallow scallop interrupts the smooth continuity of the dorsal border (Fig. 15i) and the original description should be corrected, thusly.

#### KEY TO WESTERN ATLANTIC SPECIES OF *Labidocera*

The species included in this regional key were assembled from Fleminger (1975), Fleminger and Moore (1977) and the new species described above. In the present context the western Atlantic region encompasses North Atlantic, South Atlantic, Caribbean and Gulf of Mexico coastal and offshore waters bordering North, Central and South America. Abbreviated morphological terms used in the key are defined as follows. A1: first antenna. B1, B2: first and second proximalmost segments of swimming legs. P1, P2, . . . , P5: first, second, . . . , fifth pair of swimming legs. Re1, 2, . . . : exopodal segments of appendages numbered in proximal to distal sequence. Se: spine or seta on lateral side of appendage. ThI, . . . , IV, V: segments of thorax in proximal to distal sequence. The key is limited to adult copepods distinguished by the following three features:

1. One pair of spherical lenses antero-dorsal on the forehead.
2. A rostrum divided at base of the forehead into a pair of spines that extend ventrally antero-lateral to the ventral eye.
3. P1 with a bimerous endopod and A1 with 23 or more segments.
  - 1a. Female urosome tri- or bimerous, first segment longest and widest, furca symmetrical or asymmetrical, urosome may be obscured by attached spermatophore; P5 symmetrical or nearly so, dorsal forehead lenses widely separated ..... 2
  - 1b. Male urosome pentamerous, segments similar in length; furca symmetrical; right A1 geniculated; P5 asymmetrical, exopod of right leg transformed into a large chela; dorsal forehead lenses prominent, medial margins virtually touching ..... 13
  - 2a. ThIV and V fused; P5 exopod longer than endopod; rostral spines separated by a rounded notch ..... 3
  - 2b. ThIV and V separated by articulation suture; P5 exopod shorter than endopod; rostral spines separated by a triangular notch ..... 8
  - 3a. Genital pore lateral on genital segment; total length usually exceeding 3.2 mm ..... 4
  - 3b. Genital pore ventral on genital segment; total length usually less than 2.8 mm ..... 5
  - 4a. Genital pore opening on left side; furca symmetrical; forehead without crest; tropical, oceanic, outer neritic ..... *nerii*
  - 4b. Genital pore opening on right side; furca asymmetrical; forehead with low rounded anterior crest; tropical-subtropical, oceanic, outer neritic ..... *acutifrons*
  - 5a. Right furcal ramus nearly twice the length of left ramus; ThV corners extending posteriad but not flaring laterad; anal segment distinct from middle segment of urosome; urosome usually covered by spermatophore; broadly tropical and following coastlines of Caribbean region extending to warm temperate of North America ..... *scotti*
  - 5b. Furcal rami symmetrical; ThV corners extending postero-lateral; anal segment fused to middle segment of urosome; presence of spermatophore infrequent ..... 6
  - 6a. Genital segment with patches of spinules on left and right sides; lengths of furcal rami and second urosomal segment similar, furcal rami in lateral view lacking constriction ..... 7
  - 6b. Genital segment lacking spinules; furcal rami longer than second urosomal segment; rami in

- lateral view constricted at midlength; following tropical coastlines of Central and South America ranging to warm temperate Argentina ..... *fluviatilis* a&b
- 7a. Right side of genital segment in dorsal view with low swelling ending abruptly in shoulder at about segment's midlength; following temperate coast of South America ..... *darwinii*
- 7b. Right side of genital segment lacking shoulder; following temperate coast of North America ..... *aestiva* a&b
- 8a. ThV corners strongly asymmetrical, one side reaching to posterior end of genital segment; furca asymmetrical ..... 9
- 8b. ThV corners weakly asymmetrical, left and right processes not extending beyond mid-length of genital segment in dorsal view; furca symmetrical or asymmetrical ..... 10
- 9a. Right ThV produced as slender straight spine extending to right posterior corner of genital segment, apex opposes digitiform process extending from genital segment; left ThV short, ending in a minute denticle; tropical, coastal, Barbuda Island ..... *barbudae*
- 9b. Right ThV produced as slender sinuous spine reaching to about mid-length of genital segment, latter lacking process on right side; left ThV corner produced as robust cone extending to left furcal ramus; tropical, coastal, Lesser Antilles ..... *barbadiensis*
- 10a. ThV corners short and with pronounced asymmetry, spiniform right process extending latero-posteriad ..... 11
- 10b. ThV corners short, almost symmetrical, spiniform process of left and right sides extending posteriad ..... 12
- 11a. Furca symmetrical, genital segment asymmetrical, in dorsal view with robust bilobate swelling on right side, gonopore opening ventrad; tropical, coastal, Panama ..... *panamae*
- 11b. Furca asymmetrical, right ramus broader and longer than left; genital segment asymmetrical, gonopore on left side posterior and opening dorsally; tropical Florida coast, Belize ..... *mirabilis*
- 12a. Right side of genital segment in dorsal view with triangular process; tropical, coastal, Antigua, Nicaragua, Honduras and Gulf of Honduras ..... *antiguae*
- 12b. Right side of genital segment in dorsal view with two small rounded swellings, one anterior, one posterior; tropical, coastal, Bahama Islands ..... *wilsoni*
- 13a. ThIV and V fused; rostral spines separated by rounded notch; right A1 with segment 22 lacking spur ..... 14
- 13b. ThIV and V separated by articulation suture; rostral spines separated by triangular notch; right A1 with segment 22 bearing antero-distal spur ..... 19
- 14a. Left P5 with modified endopod; right A1 with segment 17 elongated and modified to accept overlapping denticulated process extending proximad from segment 18 ..... 15
- 14b. Left P5 lacking endopod; right A1 with segment 17 unspecialized and segment 18 not overlapping segment 17; tropical, oceanic, outer neritic ..... *nerii*
- 15a. Forehead with low rounded frontal crest; total length usually exceeding 3 mm; chela with Re2 and Re3 separate; tropical-subtropical, oceanic, outer neritic ..... *acutifrons*
- 15b. Forehead lacking crest; TL usually less than 2.5 mm; chela with Re2 and Re3 fused ..... 16
- 16a. ThV corners strongly asymmetrical, right side reaching posteriad to third urosomal segment and curving ventrad; left P5 exopod with apical segment about as long as broad and bearing three similar short robust spines; chela with width of fixed finger on proximal segment (Re1) or of opposing movable finger (Re2 and Re3) less than width of remainder of proximal segment containing musculature; broadly tropical and following coastlines of Caribbean region extending to warm temperate of North America ..... *scotti*
- 16b. ThV corners weakly asymmetrical, right side reaching to second urosomal segment and straight; left P5 with apical segment elongated and bearing three slender unequal spines; right P5 chela with width of fingers equal to or exceeding width of muscular portion of proximal segment ..... 17
- 17a. Left P5 with first segment of exopod twice as long as modified endopod; furcal rami longer than combined lengths of urosomal segments three to five and dorso-ventrally constricted at about mid-length; chela of right P5 elongated, combined basal widths of processes extending from fixed finger less than half length of portion lacking processes; tropical coastlines of Central and South America ..... *fluviatilis* a&b
- 17b. Left P5 with first segment of exopod about equal in length to modified endopod; length of furcal rami less than lengths of urosomal segments three to five and not dorso-ventrally constricted; chela robust, basal width of processes on fixed finger more than half the length of portion lacking processes ..... 18
- 18a. Right ThV process in dorsal view with small abruptly stepped shoulder on medial margin; chela with processes on fixed finger not overlapping; following temperate coast of South America ..... *darwinii*
- 18b. Right ThV process in dorsal view lacking abruptly stepped shoulder; chela with processes on fixed finger overlapping; following temperate coast of North America ..... *aestiva* a&b

- 19a. Right A1 with segment 17 bearing two anterior rows of spiniform, widely spaced teeth; length of left P5 reaching to mid-length of B2 of right leg; tropical Florida coast, Belize ..... *mirabilis*
- 19b. Right A1 with segment 17 produced anteriorly as a single robust spur; left P5 about as long as right leg omitting chela ..... 20
- 20a. P5 chela with distal end of movable finger attenuated, apex reaching beyond place of proximal process on fixed finger to articulation with the basis (B2); exopod of left P5 bent medially at an angle of  $\approx 50^\circ$ ; elongated tubiform spine on right P2 Re2 bent laterally at an angle of  $\approx 50^\circ$  ..... 21
- 20b. P5 chela with distal end of movable finger short, apex not extending beyond proximal process of fixed segment; exopod of left P5 bent medially at an angle of  $\approx 35^\circ$ ; elongated tubiform spine of right P5 Re2 bent laterally at an angle of  $\approx 35^\circ$  ..... 23
- 21a. Right A1 with spur on segment 22 as long or longer than combined length of two following segments; fixed segment of P5 chela with a subequal pair of overlapping proximal processes or process vestigial; terminal segment of left P5 ending in large digitiform process roughly paralleling lateral spiniform process; lateral process exceeds length of its two distalmost lateral spines ..... 22
- 21b. Length of spur on segment 22, right A1, about half combined length of two following segments; fixed segment of P5 chela with single robust spurlike proximal process; terminal segment of left P5 with medial digitiform process diverging mediad from low rounded lateral process, lateral process much shorter than its two distalmost lateral spines; tropical, coastal, Panama ..... *panamae*
- 22a. Chela with proximal process of fixed finger in form of a subequal pair of overlapping spurs, when adducted apex of movable finger rests in notch formed by pair of spurs, fixed finger lacking narrow lamelliform process on posterior side near articulation with movable finger; tropical, coastal, Lesser Antilles ..... *barbadiensis*
- 22b. Chela with proximal process of fixed finger reduced to low bilobed knob; fixed finger with narrow lamelliform process on posterior side near articulation with movable finger; tropical, coastal, Barbuda Island ..... *barbuda*
- 23a. Fixed finger of chela with simple spiniform process opposing apex of movable finger; right ThV corner ending in a minute denticle; tropical, coastal, Bahama Islands ..... *wilsoni*
- 23b. Fixed finger of chela with spiniform process broadly triangular and expanded at base in low rounded ridge, apex of movable finger when adducted crosses notch between higher triangular and lower rounded processes; right ThV corner produced in a stout spiniform process; tropical, coastal, Antigua, Nicaragua, Honduras and Gulf of Honduras ..... *antiguae*

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